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CASTRATION IN RELATION TO THE SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS[1]

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STATION FOR EXPERIMENTAL EVOLUTION

Introduction.—It has often been observed, in many sexually dimorphic species of birds, that a female occasionally occurs which exhibits many of the characters of her mate. Frequently associated with this condition are alterations, more or less pathological, in the ovary. It has been said also that the male sometimes, and in particular the unsexed male of the domestic fowl, presents characters resembling those of the female. However, it has been pointed out that the supposed resemblance to the female can also be interpreted as due to the failure of the development of the normal adult male characters. In other words, these modified males may be referred to either a juvenile or to a female condition.

These considerations led, then, to the following questions. Will removal of the ovary from the young female fowl cause her to assume the characters of the male? Will removal of the testes from the young male cause him to assume any female characters or will it cause him to retain his own juvenile characters or will it be without effect? For answers the Brown Leghorns seemed to furnish particularly favorable material, because: first, the adult plumage, which is strongly sexually dimorphic, is practically identical with that of the Jungle fowl; second, the comb of the female, while proportionally smaller than that of the male, is larger than that of the male of many other varieties; third, there are at least three distinct stages in the development of the young bird's plumage before the adult color is reached. The first two stages do not exhibit sexual dimorphism, nor are they identical with that of the adult female. Sexual dimorphism appears first in the third juvenile plumage. At this stage, while the young female rather closely resembles the adult female, the young males in their *tout ensemble* are distinct from either the adult male or female, though sometimes feathers like those of the female may be found. A study of the characters of the Brown Leghorn capon or poullard, therefore, should show whether their characters are juvenile, male or female. For most characters, the results obtained from a preliminary set of experiments are clear cut.

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[1] This paper with some changes was read before the American Society of Naturalists at Princeton, N. J., December 28, 1911. Since then the experimental results have been fully verified. Male characters have developed on 25 females, following ovariotomy. A complete account of the newer experiments will be published later.

Description of the Secondary Sexual Characters.—In Table I is given a comparative statement of the more pronounced secondary sexual characters common to nearly all races of domestic chickens. There are other differences between the sexes, which are more subtle and therefore not considered here. In Table II are given other secondary sexual characters found in the Brown Leghorns but not in all other races of chickens.

Comment on Tables.—Such exceptions to the general statements given in Table I as occur, are mainly negative, that is, they are characters which for one reason or another do not become patent, as for example, the failure of the whole or a part of the color pattern to become visible, particularly in the case of uniformly colored birds.

In considering plumage characters aside from shape of feather there are three features to be taken into account. First, the localization of color in certain definite regions of the body, thus forming the body pattern; second, the localization of color on definite regions of the feather, forming the feather pattern; third, the pigments themselves, which are associated with each pattern in various ways.

It is rather striking, that in spite of the numerous

TABLE I[2]

A Comparative Statement of the Chief Secondary Sexual Characters of Domestic Chickens, Common to Nearly All Varieties

	Adult		Young of Both Sexes
	Male	Female	
Size, including comb	Relatively large.	Relatively small.	
Spurs	Well developed.	Absent.	
Plumage form	Hackle and saddle feathers long, narrow, pointed at tip.	Hackle feathers similar to those of male but relatively shorter and more rounded at tip; saddle feathers broad, relatively short and broadly rounded at tip.	Similar to female.
	Barbules absent on distal half of barbs of hackle, back, saddle, and wing bow feathers. Cf. Fig. 3, *A*.	Barbules absent from distal third of hackle feathers only; present elsewhere. Cf. Fig. 3, *D*.	Barbules present.
	Tail coverts, including sickles, long, curved and pointed.	Tail coverts, relatively short, broad and rounded at tips.	Similar to female.
Body color pattern	Numerous distinct color areas; viz., hackle, cape, back, saddle, wing front, wing bow, wing bay, wing bar, primaries, tail, breast and ventral surface.	Relatively few areas; viz., hackle, tail, primaries, (wing bay?), breast, ventral surface, and remainder of body.	Varies with different breeds.
Feather pattern	Usually uniform[3] or with central stripe.	Stippled or penciled when not like that of the male.	Varies with different breeds.
Behavior	Relatively erect carriage, pugnacious, frequently crows, rarely "sings," appears to lack brooding instinct.	Relatively horizontal carriage, not pugnacious, does not crow, but "sings" a great deal when in laying condition, has brooding instinct.	Peeps for a time, then follows a period when voice is rarely used until approaching maturity.

varieties of domestic chickens, there is, with one exception, only one basic *body* pattern, that of the Jungle fowl. (See table.) All other patterns, with the exception of the white crest of certain Polish, must be considered as modi-

[2] These tables make no pretense of giving all the characters which differ in the two sexes. I have also ignored minor details in some characterizations.

[3] Uniform, except as the under color can be distinguished from the surface color. See also text.

fications of the Jungle, usually by the loss or non-development of a part. I know of no other distinctive pattern in chickens, such as, for example, that exhibited by the Mallard in ducks.

TABLE II[2]

A COMPARATIVE STATEMENT OF THE CHIEF SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS, OTHER THAN THOSE GIVEN IN TABLE I

	Adult		Juvenile (Third Stage)	
	Male	Female	Male	Female
Comb	Erect. Blade proportionately large.	Lops. Blade proportionately small.	Erect. Relatively large and of quick growth.	Erect. Relatively small and of slower growth.
Spurs	Present.	Usually absent, but frequently present in various conditions of development.		
Plumage color	Hackle, reddish orange, with black central stripe; back and wing bow, dark crimson; saddle, reddish orange, often with black central stripe; wing bay, red; dorsal white area at base of tail; rest of body black.	Hackle, yellow, with dark-brown central stripe; breast, salmon; tail, primaries and concealed portions of secondaries, black; rest of body, dark and light brown, intermingled in pepper and salt fashion.	Mostly black, each feather being splashed with various amounts of red. Feathers of back often like those of young female. Body pattern of adult more or less clearly indicated.	Similar to adult but markings coarser.

The feather patterns fall into two groups, viz., those associated with sexual dimorphism and those not so associated. In the male there is no pattern of the first group. But penciling of the type found in the Dark Brahma female appears never to occur in the male and therefore belongs in the second class. Stippling is also usually distinctive of the adult female, but it occurs in the young male and under certain conditions (heterozygosis) in the adult male. In the Jungle female the stippling often approaches very closely the form of narrow concentric lines or vermiculations. Possibly the stippling of the Brown Leghorn female is due to the breaking up of such vermiculations and so is not strictly comparable with that due to heterozygosis. However this may be, stippling is normally a female or a juvenile male character. The males corresponding to these two types of females usually have uniformly colored feathers ventrally. The dorsal regions are less constant in type, being usually uniformly colored or else striped. In other breeds the feather pattern may be alike in the two sexes.

The question of behavior depends upon so many conditions, that only a few of the numerous reactions have been mentioned in the table.

The following comments are intended to apply only to Brown Leghorns.

While the comb of the female usually lops to one side or the other, it does not always do so. There are indications, moreover, that by proper matings this character could be transferred to the male.

Spurs are usually absent from the female, yet they are occasionally well developed. Their presence can not be taken as a certain indication of the assumption of a male character by the female, for there was an old Scottish race in which both sexes were spurred. Nor need they indicate the presence of an abnormal ovary, for in one case in which they had become well developed at 9 months of age, the hen proved to be a splendid layer. These spurred hens are probably due to the presence or absence in the germ plasm of some definite determiner, as certain of my breeding experiments indicate.

The plumage color within certain limits is variable, so that it is a little difficult to describe briefly. American fanciers recognize only one type of plumage color for each sex, that described in the "American Standard of Perfection," but beside the "Standard" female there is one in which the salmon breast is replaced by one of nearly the same color as the back. Beside the "Standard" male is one in which the striping of the hackle and saddle feathers is lost, and third, one in which there is some red in the under parts. It is evident, moreover, from experiments in cross breeding, that the body pattern of the Brown Leghorn is not a unit, but is composed of several parts.

These departures from the ideal and the probable variability in the gametic constitution of supposedly purebred stock may be expected to influence the behavior of the birds under castration. They indicate also that a character which at one time may behave as a secondary sexual character, at others forms a normal character of both races.

Experimental.—Without taking time to describe the details of the experiments, except to note that the gonads were removed from the chicks when they were 21–28 days old, that is, they were much younger than is the case in commercial caponization, we may proceed directly to a consideration of the results, taking up first the effects of castration on the male.

Seven of the castrated males reached four months of age, then three were accidentally killed. The autopsies on these three showed an entire absence of testicular material in two cases. The third had a tiny nodule, possibly testicular, on the mesentary near the former site of the testis.[4] All four survivors were kept until they were 16 months of age. Two were then killed for study. They developed the normal plumage of the male and were it not for the small comb and wattles they would have had nearly the same appearance as a normal cock (Fig. 1). They are, however, somewhat fuller plumaged and rather heavier looking birds than a normal cock. The spurs are well developed but on the other hand these capons are less active in their movements, are non-combatants and show no sexual instincts. They have never been heard crowing, though they may be made to squawk or even cluck like a *cock*.

One of these capons was somewhat anomalous in that he had much the same appearance as a normal cock. He had a large comb but did not crow. At one time he showed some inclination to pay attention to the hens, but as far as I was able to observe, it never went as far as an attempt at copulation. At the autopsy it was found that there had been an autoplastic transplantation of a bit of the testis.

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[4] Unfortunately this material was not sectioned.

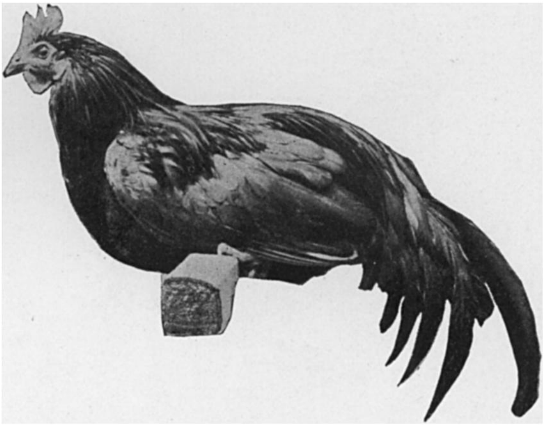

FIG. 1. Brown Leghorn Capon. The colors are exactly those of the male as given in Table II.

It will have been observed from the foregoing description, that the small comb of these capons is the only character which might be considered female. In all other points the characters of the capon are the characters of the cock, sometimes exaggerated (feather length), sometimes infantile (crowing instinct). None are positively female, except perhaps the comb, which is much too large to be purely infantile, and too small and of the wrong proportions to be that of a normal adult female. On the whole it most closely resembles that of the *mature young female* before she has actually commenced to lay, or of the adult female when out of laying condition. Comb size is affected by so many conditions that the question as to whether or not the capon has a female type of comb is not easily answered, and therefore must await further studies.

We may turn now to the effects of castration on the female. Unfortunately, only one of the females from which the ovary (naturally only the left, since it was assumed that the right had completely degenerated) was removed, reached maturity. There is no doubt as to the effect of ovariotomy on this individual (Fig. 2), which commonly passed as a cock, with those unacquainted with the bird's history. Nevertheless, the assumption of male characters has not been quite complete, as is shown by a consideration of the following features. First, the presence of feathers on the back which are very much hen-like (Fig. 3, *B*). Second, the wing bow is poorly developed. Third, the shank is too short for that of a cock. In some points of behavior, such as lack of the crowing instinct, non-combativeness, cackle and general indifference to the hens, she is hen-like. On the other hand, her carriage is cock-like and by suitable means she has been made to cluck like a cock and even to pay a little attention to the hens, though this last reaction was produced only once or twice. The peculiar shape and carriage of the tail probably has nothing to do with the effects of castration, since this bird had only half a rump. Moreover, a rumpless cock occurred in this same strain.

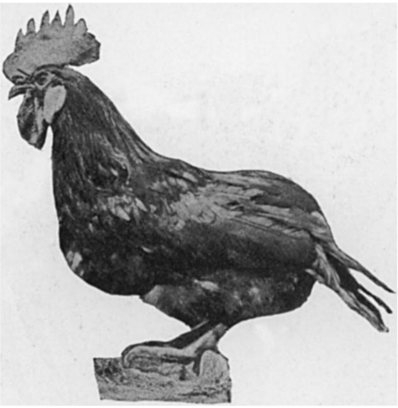

FIG. 2. Female Brown Leghorn from which the ovary was removed. The colors, with the exception of some feathers as noted in the text, are those of the *male* as given in Table II. The long saddle feathers are hidden by the wing, but see Fig. 3, *C*.

Some additional light on the question is afforded by the effect produced by castration on a second female, which died at the age of four months. When the first feathers of the third stage began to appear, they were like those of the young male. The later feathers, however, were those of the normal female. The explanation of this anomalous behavior was found at the autopsy, for it showed the presence of an ovary about one half the size of that of a normal chick of the same age. As long as the ovary or its normal secretion was practically absent, the development of this female was along lines similar to that of the male, but with the regeneration of the ovary development returned to its usual course.

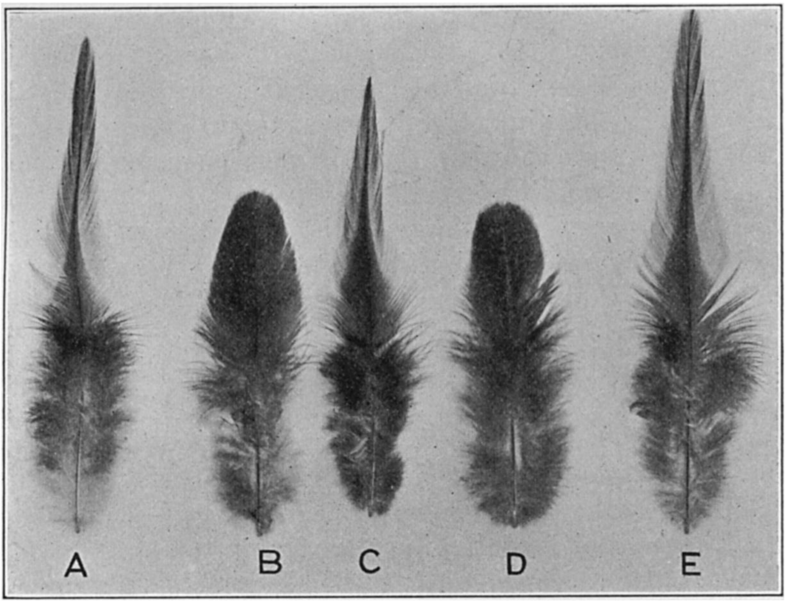

FIG. 3. Feathers from the saddle region of the various types of birds described. *A*, normal male; *B* and *C*, two sorts of feathers from the bird shown in Fig. 2; *D*, normal female; *E*, capon.

These experiments, then, indicate clearly that while the female may assume male characters following the removal of the ovary, the male assumes no positive female characters after removal of the testes.

Theoretical.—Certain of my breeding experiments have seemed to show that the Brown Leghorn plumage colors and pattern followed a sex-limited mode of descent. Certain difficulties, however, have arisen. As stated above, it has become evident that the coloration and pattern of the Brown Leghorns is not due to a single inheritable unit, but to a complex. This means that its more or less independent parts must be discovered and the mode of inheritance as well as the conditions under which each part becomes visible in the soma, worked out. Until this is done it will be impossible to say what part sex-limited inheritance plays in determining sexual differences. The following representation, then, is merely an attempt to formulate a working hypothesis.

The male may be considered to be duplex for an internal secretion S, produced by the testes, which is necessary for the full development of the comb and less clearly for the crowing instinct and sexual behavior, but not for plumage and spurs. In the female this secretion is replaced by one S' produced by the ovary. (S' may, perhaps, stand in some simple chemical relation to S.) To its effect is to be referred the female's form and color. When the ovary is removed or becomes pathological so that its normal secretion is no longer produced, then the male characters develop to an extent which is determined by factors at present unknown to us. Nor are we concerned here as to what part of the ovary or testis produces this secretion (or secretions, for S and S', respectively may well represent a number of secretions which behave in the same general way). In any case the internal secretion may be conceived to be associated with sex in the same manner as any other sex-limited character. The formula for the male would then be $S♂\ S♂$, that for the female $S♂S'♀$. S' is of course to be considered dominant to S. If this scheme represents the actual condition of affairs it may not be necessary to suppose that the female Brown Leghorn is simplex for L where L represents the whole or a part of the male Leghorn pattern complex, for *S′* might be able to transform two doses of *L* into the condition observed in the female as well as one dose. This is, however, a matter to be tested by experiment.

In insects, Meisenheimer and others have shown that castration is without effect on the secondary sexual characters of either sex. This lack of association between the secondary sexual characters and the gonads may find its explanation in the absence of a modifying secretion from these forms, the secondary sexual characters being determined solely by differences in the gametic constitution of the sexes, for example of the form *AA* in one sex and *AB* in the other, *B* being dominant over *A* and linked with the sex determiner, in the usual fashion for a sex-limited factor.[5] Secondary sexual characters of insects would then belong to a different category from those of the birds. There is some evidence, however, that certain characters of the female fowl are not under the control of the secretion of the ovary, for they do not become male-like after the removal of the ovary and therefore are like the insects in this respect. This point requires further study.

There is one more point to be considered. I have shown that in the Brown Leghorns as well as in Rouen ducks that the male does not assume female characters as a result of castration. Does the adult male of other sorts of birds ever exhibit female characters? An affirmative answer is possible only in those cases in which the juvenile plumage of the male is like that of the female. But if we consider only those cases in which the juvenile male plumage is unlike that of the female, we shall find that conclusive evidence on this point is wanting, at least I have thus far been unable to secure such evidence.

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[5] There are, of course, other ways of representing this association.